Emergence pattern, microhabitat choice, and population structure of the Maghribian endemic Gomphus lucasii Selys, 1849 (Odonata: Gomphidae) in northeastern Algeria

Rabah Zebsa, Rassim Khelifa & Amin Kahalerras

Published online: 08 Oct 2015.

Submit your article to this journal

View related articles

View Crossmark data

Emergence pattern, microhabitat choice, and population structure of the Maghribian endemic *Gomphus lucasii* Selys, 1849 (Odonata: Gomphidae) in northeastern Algeria

Rabah Zebsa[a], Rassim Khelifa[b]* and Amin Kahalerras[b]

aDépartement d'écologie et du génie de l'environnement, Faculté des Sciences de la Nature et de la Vie et des Sciences de la Terre et de l'Univers, Université 08 Mai 1945, Guelma 24000, Algérie; bDépartement de biologie, Faculté des Sciences biologiques et agronomiques, Université de Tizi Ouzou, Tizi Ouzou 15000, Algérie

Emergence of *Gomphus lucasii* Selys, 1849, an unstudied Maghreb endemic, was synchronised by overwintering in the final stadium in the Seybouse River in northeastern Algeria. Regular collections revealed that half of the annual population emerged during 10 days, showing a typical 'spring species' emergence pattern. Sex ratio was slightly male biased (51%). Males and females did not differ in vertical stratification. Emergence support choice was not random, but rather depended on support height, body size, and daily population density. Mortality was caused mainly by ants, although deformity of tenerals and bird predation were also important factors. *Gomphus lucasii* has been assessed as vulnerable (International Union for Conservation of Nature(IUCN) Red List), and the information provided in our study will be helpful in future conservation efforts.

Keywords: Odonata; dragonfly; *Gomphus lucasii*; endemic; exuviae; emergence; Algeria

Introduction

Emergence is a very important stage in the life cycle of aquatic insects characterised by the passage of individuals from aquatic to terrestrial (aerial) life. In odonates, like many other aquatic insects, individuals should choose a suitable support and leave the water to achieve the ecdysis process (Corbet 1999). At this stage, they spend a substantial time in an immobile state, vulnerable and unable to escape any predation attempt. To cope with this handicap, odonates species have evolved a variety of spatiotemporal emergence patterns by choosing the right site at the right time. In fact, many species tend to emerge at night to escape the diversity of predators that could be encountered during daytime, while others have diurnal or even mixed emergence rhythms (Corbet 1999). Therefore, site selection plays a significant role to minimise mortality risks at emergence (Banks and Thompson 1985; Gribbin and Thompson 1991; Corbet 1999; Purse and Thompson 2003). The choice of emergence sites by Odonata and other aquatic insects might be shaped by predation pressure, inducing a selection process favouring specific periods and space to avoid detection, as has been found in many vertebrates and invertebrates (Hieber 1984; Mangel 1987; Rehfeldt 1990; Magnusson and Hero 1991; Thompson and Pellmyr 1991).

Once the whole emergence process is completed, tenerals leave the final instar exuviae behind and take their first flight. Surveys have shown that exuviae provide valuable

*Corresponding author. Email: rassim.khelifa@ieu.uzh.ch

information on habitat suitability (Raebel, Merckx, Riordan, Macdonald, and Thompson 2010), sex ratio, emergence density, and temporal pattern of emergence (Corbet 1999). Moreover, Foster and Soluk (2006) demonstrated that exuviae sampling gave reliable estimation of larval population density. In addition, using this material like an indirect and non-invasive sampling method is valuable to monitor species of conservation concern. However, despite all advantages in using exuviae-based surveys they remain markedly neglected with respect to adults (Raebel et al. 2010).

Within the Mediterranean basin, only two species of dragonflies (*Cordulegaster princeps* Morton, 1915 and *Gomphus lucasii* Selys, 1849) are endemic to the Maghreb (Riservato et al. 2009). The former species is confined to the Moroccan high and middle Atlas, whereas the latter has a larger distribution ranging from Tunisia to the extreme west of Algeria (Boudot 2010). *Gomphus lucasii* (Algerian cubtail) (Odonata: Gomphidae) is currently listed vulnerable in the IUCN Red list and is one of the most unstudied gomphids in the Palaearctic. Boudot (2010) stated that 30 localities are currently known (17 in Tunisia and 13 in Algeria) and in half of them, the species is either extinct or threatened due to severe pollution and degradation of watercourses. He also claimed that no population reached 250 adults and the global population size was approximately 2500 individuals.

The purpose of our study was to investigate the temporal pattern of emergence, microhabitat choice, and seasonal regulation of *G. lucasii* in the Seybouse River (northeastern Algeria), a site known to harbour the largest population of the endangered *Calopteryx exul* Selys, 1853 in the world (Khelifa 2013).

Material and methods

Study site

This study was carried out in the Seybouse River upstream (northeastern Algeria), 5 km west of Guelma (36°28′N, 7°22′E). Two sites, approximately 1.5 km apart, were selected in which two 20-m stretches were sampled. Site 1 was consisted of stretches G7 and G10, both occurred at the main water course. Site 2 included stretch A along the main water course and stretch P at a shallow channel 300 m long. Vegetation of stretch A and P consisted of dense *Typha angustifolia* Linnaeus, 1753 while that of stretch G7 to G10 was dominated mainly by *Cyperus longus* Linnaeus, 1753, *Paspalum distichum* Linnaeus, 1753, *T. angustifolia*, *Tamarix gallica* Linnaeus, 1753, and *Salix pedicellata* Desf, 1799.

Sampling methods

Based on previous observations on the flight period of *G. lucasii* in the Seybouse River (Khelifa et al. 2011), we started daily visits along the four study stretches (A, P, G7, and G10) in mid April 2011 in order to note the exact onset of emergence. The end of emergence period was confirmed after seven subsequent visits of unsuccessful exuviae collection. Exuviae were daily collected in late afternoon (at 04:00 pm) within all stretches by intensively searching the bank vegetation, emergent stones, and soil. Final instar larvae of dragonflies may travel remarkable distance out of the water before choosing a suitable support, so areas parallel to stretches were also checked for potential exuviae (up to 5 m from water). We measured the height of the exuviae fixation (*He*) (distance from the water surface to the tip of exuviae abdomen), the height of the chosen support (*Hs*) and the distance from the water for each exuviae to the nearest 1 cm. The ratio between height

of the exuviae fixation and support height was calculated (*He*/*Hs*, hereafter). Water level was measured daily with a graduated stick in the middle of P stretch over the entire emergence season. In the laboratory, the exuviae were sexed and the body length was measured to the nearest 0.01 mm using a digital calliper. Broken or fragmented exuviae were not measured and, therefore, were not included in statistical analyses related to body size. The number of days when 50% of the population had emerged (EM50) was estimated.

One of the most defining characteristic of spring species is that most larvae overwinter in the last instar, so that their emergence in the spring will be synchronous (Corbet 1954). In such species, the three last instars are usually enough to determine the population structure and seasonal regulation of a species (Suhling 1995). Larvae were collected in October 2011, April 2012, and August 2012 with a rectangular hand net from the substrate or the bank vegetation in two different localities (P and G10). Individuals were measured (body length) in the field with a digital calliper to the nearest 0.01 mm. The percentages of final instar larvae before the winter (October) and before emergence (April) were calculated for each site. Lutz's (1968) nomination of instars was followed (F-0: final, F-1: penultimate, F-2: antepenultimate for the last three instars).

Data analysis

Statistical analyses were carried out using SPSS 17.0 software. Non-parametric tests were applied when residuals were not normally distributed. Chi-square tests were used to reveal sex ratio deviations from unity (1:1) at emergence in all study stretches. Kruskal−Wallis tests were used to detect potential significant differences in exuviae abundance, body length, height of exuviae fixation, support height, ratio *He*/*Hs*, and distance from the water between the four study stretches. Mann−Whitney *U*-tests were used to test for differences in body length, height of exuviae fixation above the water, support height, ratio *He*/*Hs*, and distance from the water between males and females. To test if body size had an effect on individual microhabitat choice, Spearman correlations were used between exuviae body length and the four following parameters: height of exuviae fixation, support height, ratio *He*/*Hs*, and distance from the water. Similarly, to search for eventual density-dependent microhabitat choice, the relationship between daily exuviae density and the latter parameters was tested. In the shallow P channel, water level usually varied daily during the emergence season. We investigated the effect of such variability on support choice by using a Spearman correlation between water level and daily number of individuals emerging on stones. Spearman correlation was also used between body length and emergence date to show if individual body size increased or decreased over the emergence season. To test if the height of exuviae fixation above the water surface depended on the support height and on its position according to the support, Spearman correlations were used between support height, height of exuviae fixation, and ratio *He*/*Hs*. Mann−Whitney *U*-test was used to compare the distances travelled from the water to terrestrial habitats by predated and non-predated larvae.

Results

Abundance and sex ratio

A total of 1247 exuviae were collected from the four study stretches. Abundance of *G. lucasii* was significantly variable between the four stretches ($\chi^2 = 42.32$, df $= 3$, $p < 0.0001$) ranging from 83 to 499 individuals (Table 1).

Table 1. Abundance and sex ratio at emergence of *Gomphus lucasii* Selys, 1849 in the four study stretches.

	A	P	G7	G10	Total
Number of exuviae	499	309	83	383	1274
Number of males	252	155	49	193	649
% males	50.5	50.16	59.03	50.39	50.94
p-value of χ^2 test	0.64	0.97	0.30	0.61	0.70

All exuviae from all stretches combined emerged within 31 days from 29 April to 30 May showing a peak on 8 May representing 14.44% of the total emergent population. Cumulative per cent of annual emergence is presented in Figure 1.

The overall EM50 was 10 days. EM50 was 9 days in stretches P, G7 and G10, but 12 days in stretch A (Table 2).
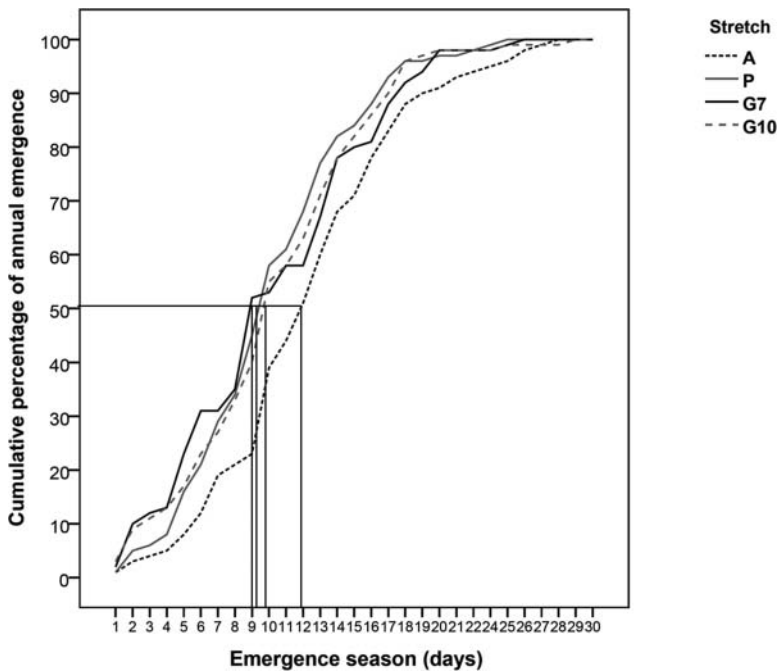

Figure 1. Cumulative percentage of annual emergence of *Gomphus lucasii* Selys, 1849 in four different stretches in the emergence season of 2011. The horizontal line is set to 50% so that the vertical lines indicate the EM50 of each stretch.

Table 2. Post-emergence time in days and date after which 50% of the annual population of *Gomphus lucasii* Selys, 1849 had emerged (EM50) at the sample stretches.

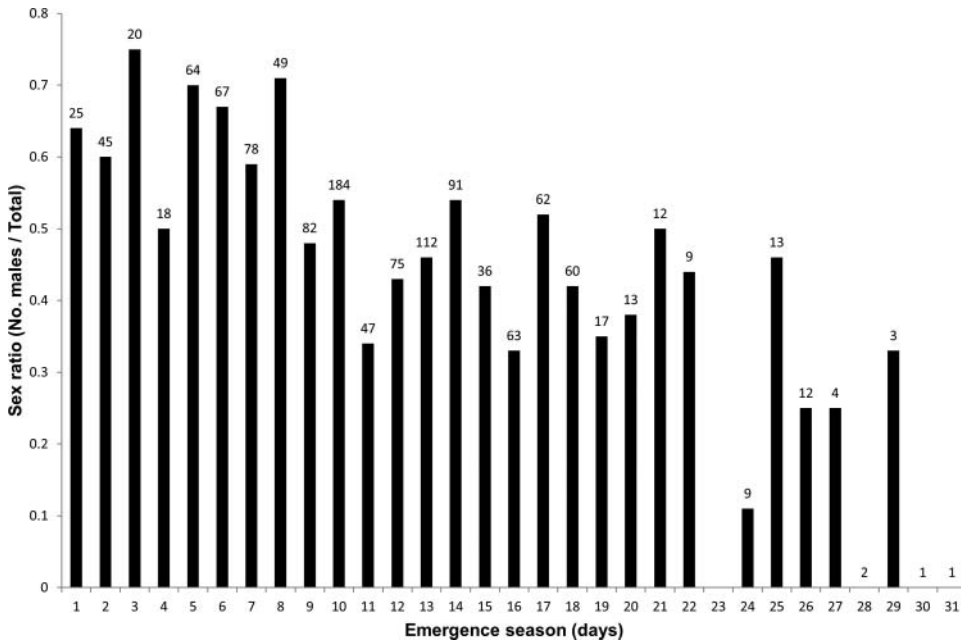|	A	P	G7	G10	Total
Days	12	9	9	9	10
Date	10 May	7 May	7 May	7 May	8 May

Figure 2. Sex ratio trend of *Gomphus lucasii* Selys, 1849 over the emergence season of 2011 for males.

Overall sex ratio at emergence as well as sex ratio at each stretch was slightly but not significantly male biased (Table 1). It was similar and approximated 50% in A, P, and G10 but slightly far from equilibrium in G 7 (59.03%). Throughout the emergence period, it was male biased early in the season then approached equilibrium in mid-season (Figure 2). EM50 of males (10 days) was 2 days earlier than that of females (12 days).

Substrate choice and vertical stratification

Female exuviae (29.79 ± 1.09 mm, $N = 504$) were significantly longer than males (28.91 ± 1.01 mm, $N = 544$) (*U*-test, $p < 0.0001$). There was a significant difference in body length between the different stretches ($\chi^2 = 54.07$, df $= 3$, $p < 0.0001$). Mean body length was 29.40 ± 1.03 mm, 29.71 ± 1.14 mm, 29.08 ± 1.21 mm, and 29.07 ± 1.17 mm in stretch A, P, G7, and G10, respectively. Body length increased significantly over the emergence season for both males ($r = 0.14$, $p = 0.001$, $N = 504$; Figure 3) and females ($r = 0.16$, $p = 0.0001$, $N = 523$; Figure 3). Among other coexisting odonate species (*Calopteryx exul*, *Platycnemis subdilatata* Selys, 1849, *Onycogomphus costae* Selys, 1885, with a few *Orthetrum coerulescens* Fabricius, 1798), *G. lucasii* was the largest species within all stretches.

Gomphus lucasii used different substrates to emerge, namely several species of helophytes (91.8%, mainly *T. angustifolia*, *Paspalum distichum*, and *Cyperus longus*), trees (1.65%, *Tamarix gallica*, and *Nerium oleander* Linnaeus, 1753), stones (1.41%), or the soil (0.55%). A small proportion was found floating on the water between stems of plants (3.14%) or setting (backward) on the ground probably after falling from surrounding supports (1.45%). Emergence on stones was only recorded at P stretch because water
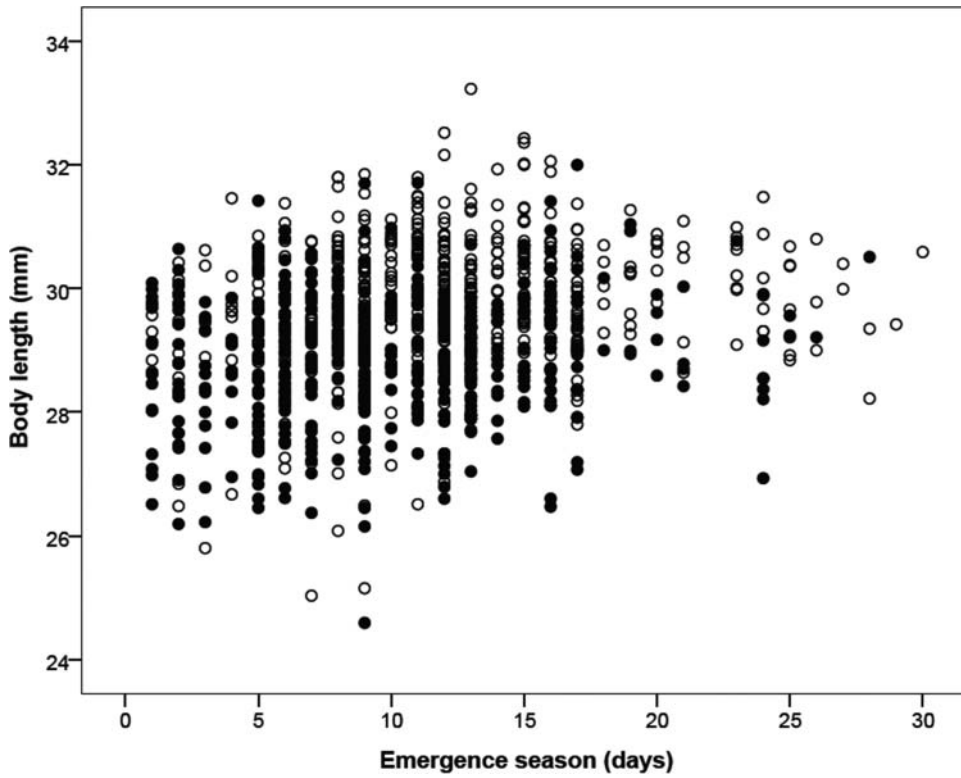
Figure 3.   Body length of *Gomphus lucasii* Selys, 1849 exuviae over the emergence season of
2011. Data of all stretches were combined. Black circles − males; open circles − females.

level of the channel often decreased and made stones appear above the water surface. A
significant negative correlation was observed between the number of individuals emerging
on stones and water level ($r = -0.76$, $p < 0.0001$, $N = 31$).

The species emerged at a mean height of 15.56 ± 17.99 cm above the water surface
with a maximum of 183 cm. The mean chosen substrate height was 57.89 ± 70.87 cm
while the mean ratio *He/Hs* was $38.47 \pm 26.55\%$. When we included only individuals
emerging out of the water, distance from the water had a mean of 51.35 ± 30.53 cm and
a maximum of 165 cm. Considering all stretches, body length was significantly positively
correlated only with exuviae support ($r = 0.1$, $p = 0.001$, $N = 981$) and negatively related
to ratio *He/Hs* ($r = -0.08$, $p = 0.006$, $N = 981$).

There was no significant difference in height of exuviae fixation (*U*-test: $p = 0.22$),
support height (*U*-test: $p = 0.23$), ratio *He/Hs* (*U*-test: $p = 0.82$), and distance from the
water (*U*-test: $p = 0.07$) between males and females. However, a significant difference
between stretches of the latter variables resulted (Kruskal−Wallis test: $p < 0.0001$, for
all variables). Support height was positively correlated to height of exuviae fixation
($r = 0.56$, $p < 0.0001$, $N = 1096$) and negatively related to the ratio *He/Hs* ($r = -0.46$,
$p < 0.0001$, $N = 1096$). Height of exuviae fixation, support height, and distance from the
water were positively correlated to daily exuviae density ($r = 0.16$, $p < 0.0001$,
$N = 1096$; $r = 0.14$, $p < 0.0001$, $N = 1096$; $r = 0.07$, $p = 0.02$, $N = 1096$, respectively).

Mortality at emergence

Predation and deformity of tenerals were the two main sources of mortality during this study. We observed 13 cases of mortality due to ants killing individuals before the end of the ecdysis process. Distances travelled by those larvae (65.02 ± 41.25 cm, $N = 13$) were significantly longer than those that were not predated by ants (41.54 ± 25.56 cm, $N = 101$) ($U = 180.5$, $p < 0.0001$) which reveals that the farther the distance from the water the higher the predation probability by ants. After adults left their exoskeleton and dried, they flew high, heading for terrestrial habitats far from the water. At this moment, we observed three cases of predation by large asilids. In addition, many avian predation attempts by barn swallows (*Hirundo rustica* Linnaeus, 1758) and domestic sparrows (*Passer domesticus* Linnaeus, 1758) were recorded but only one sparrow was observed to successfully capture a teneral individual in flight. Five cases of teneral wing deformation were noted mainly during the peak of emergence (between 6 and 10 May). Deformed individuals were unable to perform a short flight and were probably condemned to die soon afterwards. Another important source of mortality was flooding as the one observed on 21 May 2011 when no exuviae were collected. However, we could not quantify its contribution to the overall mortality.

Population structure

A total of 67 (26 in October and 41 in April) and 35 (18 in October and 17 in April) larvae were collected from G and P, respectively. Figure 4 presents percentage distribution of *G. lucasii* in the last three stadia before the winter and emergence at two different sites.
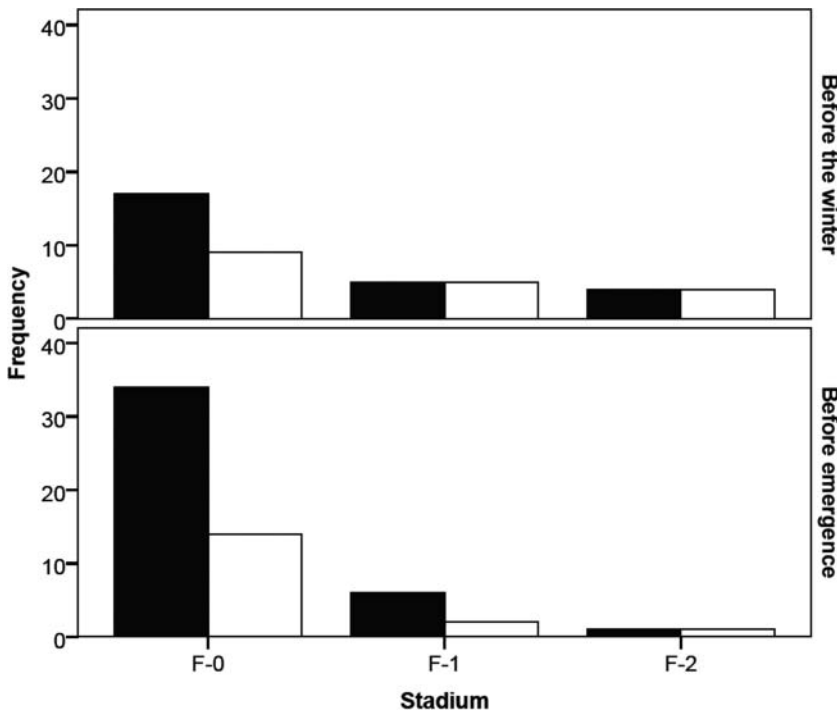

Figure 4.   Percentage distribution of *Gomphus lucasii* Selys, 1849 larvae in the last three instars in two different sites in October and April. Black bars − site G; open bars − site P.

At G, most larvae (65.38%) reached the final stadium larva before the winter while a larger proportion (82.93%) was recorded before emergence. At P, a similar trend was observed with 50% of larvae reaching the final stadium whereas 82.35% were in the latter state before emergence. There was no significant difference in the frequency distribution of the last three larval instar between sites in October (*U*-test: $p > 0.05$) and April (*U*-test: $p > 0.05$). No larvae were collected in July and August, indicating that all larval population emerges after one year of development (univoltine species).

Discussion

Gomphus lucasii showed a synchronous emergence pattern which is typical of 'spring' species. The annual duration of emergence lasted one month with an overall EM50 of about 10 days. Extreme cases of emergence synchrony, in which the annual larval population emerges in a single day, have been recorded for *G. vulgatissimus* Linnaeus, 1758 (Martin 1895; Wesenberg−Lund 1913) and *G. vastus* Walsh, 1862 (Johnson 1963). Variability in EM50 between stretches (habitats) was not as notable as the one observed in *Onychogomphus uncatus* Charpentier, 1840 in southern France (Suhling 1995) and *Pyrrhosoma nymphula* Sulzer, 1776 in northern England (Gribbin and Thompson 1991), probably because all stretches occurred in the same watercourse and were probably subject to similar environmental conditions.

As observed in many other studies on odonates, there were no substantial differences in the emergence pattern between sexes in the study population. Corbet and Hoess (1998) found that sex ratio at emergence was usually female biased in anisopterans in contrast to zygopterans. Similarly, a study on three gomphids (*G. flavipes* Charpentier, 1825, *G. vulgatissimus*, and *Ophiogomphus cecilia* Fourcroy, 1785) showed a female-biased sex ratio at emergence (Kalniņš 2006). However, the current study on *G. lucasii* showed different results with a slightly male-biased sex ratio which could be explained by minor differences in larval survival between sexes due to either sex-biased activity, i.e., one sex (female) was more active than the other (Baker, Forbes, and Proctor 1992) or sexual size dimorphism, i.e., females were larger than males (Purse and Thompson 2003).

We found out that both females and males showed a trend of increasing size throughout the emergence season. This finding was different from many observations made on several temperate species, showing a negative relationship between body size and emergence date (Banks and Thompson 1985; Michiels and Dhondt 1990; Corbet 1999; Purse and Thompson 2003). A study on a Japanese species of Libellulidae, *Deiela phaon* Selys, 1883 showed similar results, although sample size was very small (Sugimura 1983). One explanation might be the size-dependent mortality in early emergence season.

Boudot (2010) claimed that both the Algerian and Tunisian populations of *G. lucasii* have decreased severely during the last century. Our regular sampling of 60 m of shoreline (all stretches combined) in upstream Seybouse allowed us to count 1247 exuviae, approximately half the entire global population as estimated by Boudot (2010). This result highlights the inaccuracy of earlier estimations usually based on non-rigorous methodology (punctual observations on non-marked adults). According to our knowledge on larval occurrence in the Seybouse River, the local population size could easily reach 10,000 individuals and it could be multiplied by five when we consider the entire watershed.

Vertical stratification of *G. lucasii* (15.56 ± 17.99 cm) was similar to other gomphids like *G. pulchellus* Selys, 1840 (17.75 ± 9.18 cm) and *Onychogomphus uncatus* (17.40 ± 4.27 cm) (Cordero 1995). Dragonflies are suspected to choose carefully their emergence

site for many reasons related to intraspecific competition, predation, or microclimate (Cordero 1995). Starting from this principle, it is reasonable to think that larvae choose emergence height based on the total height of the support. To our knowledge, the two latter parameters have not been considered previously in studies of vertical stratification.

There was no relationship between body length and vertical stratification of *G. lucasii* exuviae. However, larger individuals chose longer supports and tended to hold lower positions with respect to the support height. A possible explanation is that longer supports (mainly reeds) are usually thicker and can carry larger dragonfly larvae. Regardless of body size, height of exuviae fixation and position clearly depended on the support height. The data suggest that emerging larvae climbed higher when the support was long, but not so high as to become unstable or to be unable to avoid wind turbulence during ecdysis. Vertical stratification between sample stretches differed because of vegetation differences, from short *Paspalum distichum* to long *Typha angustifolia*. Moreover, daily emerging larva density had also an effect on individual behaviour at emergence because it was positively correlated to the height of exuviae fixation, support height, ratio *He/Hs*, and distance from the water. In fact, during the peak of emergence final instar larvae chose higher positions, supports, ratios *He/Hs*, or even places out of the water to avoid high competitive pressure induced by conspecifics (Corbet 1999). In that way, deformity caused by conspecifics which induces mortality (Purse and Thompson 2003) could be avoided.

Sources of mortality during and after emergence recorded in this study were already observed in other surveys dealing with different Odonata species (Gribbin and Thompson 1991; Corbet 1999; Bennett and Mill 1993; Purse and Thompson 2003) but in our study, proportion of dead individuals compared to the population size (1.7%) was smaller. Consistent with our study, it has been suggested that natural mortality at emergence does not produce a substantial effect on the population dynamics as does mortality during the larval and adult periods of odonate life (Ubukata 1981). However, anthropogenic factors like regular flooding caused by dam release over the emergence season could result in a significant decrease in local population size.

Odonate voltinism has been shown to be governed by two main latitude-dependent factors, namely temperature and photoperiod (Corbet, Suhling, and Soendgerath 2006). In general, the higher the latitude, the longer the life cycle. Data available on Palaearctic gomphids showed that most species complete a single generation in at least two years (Corbet et al. 2006). One exception is *Paragomphus genei* Selys, 1841 which is said to be univoltine in southern Spain (Testard 1975). However, studies in North Africa where latitudes are closer to the equator have never been carried out. The present study showed that *G. lucasii* whose geographic range is characterised with a Mediterranean climate is a univoltine species. It might be expected that populations existing in high altitude areas could be partially semivoltine.

In conclusion, our study highlighted new data on the biology and seasonal regulation of *G. lucasii* in northeastern Algeria. Considering the fact that other populations were also observed along the whole watershed (Khelifa et al. 2011), it might be interesting to conduct a large scale sampling in the Seybouse River watershed in order to more accurately estimate population trends, and we expect that the total population size of the Seybouse watershed far exceeds the current global population claimed by IUCN experts.

Acknowledgements

References

Baker, R.L., Forbes, M.R., and Proctor, H.C. (1992), 'Sexual Differences in Development and Behaviour of Larval Ischnura Verticalis (Odonata: Coenagrionidae)', *Canadian Journal of Zoology*, 70, 1161−1165.

Banks, M.J., and Thompson, D.J. (1985), 'Lifetime Mating Success in the Damselfly Coenagrion Puella', *Animal Behaviour*, 33, 1175−1183.

Bennett, S., and Mill, P.J. (1993), 'Larval Development and Emergence in Pyrrhosoma Nymphula (Sulzer) (Zygoptera: Coenagrioidae)', *Odonatologica*, 22, 133−145.

Boudot, J.-P. (2010), 'Gomphus Lucasii'. www.iucnredlist.org.

Corbet, P.S. (1954), 'Seasonal Regulation in British Dragonflies', *Nature*, 174, 655.

Corbet, P.S. (1999), *Dragonflies: Behaviour and Ecology of Odonata*. Colchester: Harley Books.

Corbet, P.S., and Hoess, R. (1998), 'Sex Ratio of Odonata at Emergence', *International Journal of Odonatology*, 1, 99−118.

Corbet, P.S., Suhling, F., and Soendgerath, D. (2006), 'Voltinism of Odonata: A Review', *International Journal of Odonatology*, 9, 1−44.

Cordero, A. (1995), 'Vertical Stratification During Emergence in Odonates', *Notulae Odonatologicae*, 4, 103−105.

Foster, S., and Soluk, D. (2006), 'Protecting More Than the Wetland: The Importance of Biased Sex Ratios and Habitat Segregation for Conservation of the Hine's Emerald Dragonfly, Somatochlora Hineana Williamson', *Biological Conservation*, 127, 158−166.

Gribbin, S.D., and Thompson, D.J. (1991), 'Emergence of the Damselfly Pyrrhosoma Nymphula (Sulzer) (Zygoptera: Coenagrionidae) from Two Adjacent Ponds in Northern England', *Hydrobiologia*, 209, 123−131.

Hieber, C.S. (1984), 'Egg Predators of the Cocoons of the Spider Mecynogea Lemniscata (Araneae: Araneidae): Rearing and Population Data', *Florida Entomologist*, 67, 176−178.

Johnson, C. (1963), 'A Note on Synchronized Emergence in Gomphus Vastus Walsh (Odonata: Gomphidae)', *The Canadian Entomologist*, 95, 69−69.

Kalniņš, M. (2006), 'The Distribution and Occurrence Frequency of Gomphidae (Odonata: Gomphidae) in River Gauja', *Acta Universitatis Latviensis*, 710, 17−28.

Khelifa, R. (2013), 'Flight Period, Apparent Sex Ratio and Habitat Preferences of the Maghribian Endemic Calopteryx Exul Selys, 1853 (Odonata: Zygoptera)', *Revue d'écologie*, 68, 37−45.

Khelifa, R., Youcefi, A., Kahlerras, A., Al Farhan, A., Al-Rasheid, K.A., and Samraoui, B. (2011), 'L'odonatofaune (Insecta: Odonata) du bassin de la Seybouse en Algérie: intérêt pour la biodiversité du Maghreb', *Revue d'écologie*, 66, 55−66.

Lutz, P.E. (1968), 'Effects of Temperature and Photoperiod on Larval Development in Lestes Eurinus (Odonata: Lestidae)', *Ecology*, 49, 637−644.

Magnusson, W.E., and Hero, J.-M. (1991), 'Predation and the Evolution of Complex Oviposition Behaviour in Amazon Rainforest Frogs', *Oecologia*, 86, 310−318.

Mangel, M. (1987), 'Opposition Site Selection and Clutch Size in Insects', *Journal of Mathematical Biology*, 25, 1−22.

Martin, R. (1895), 'Une éclosion de libellules', *Feuille des Jeunes Naturalistes*, 25, 141−142.

Michiels, N.K., and Dhondt, A.A. (1990), 'Costs and Benefits Associated with Oviposition Site Selection in the Dragonfly Sympetrum Danae (Odonata: Libellulidae)', *Animal Behaviour*, 40, 668−678.

Purse, B.V., and Thompson, D.J. (2003), 'Emergence of the Damselflies, Coenagrion Mercuriale and Ceriagrion Tenellum (Odonata: Coenagrionidae), at Their Northern Range Margins, in Britain', *European Journal of Entomology*, 100, 93−100.

Raebel, E.M., Merckx, T., Riordan, P., Macdonald, D.W., and Thompson, D.J. (2010), 'The Dragonfly Delusion: Why It is Essential to Sample Exuviae to Avoid Biased Surveys', *Journal of Insect Conservation*, 14, 523−533.

Rehfeldt, G. (1990), 'Anti-Predator Strategies in Oviposition Site Selection of Pyrrhosoma Nymphula (Zygoptera: Odonata)', *Oecologia*, 85, 233−237.

Riservato, E., Boudot, J.P., Ferreira, S., Joviæ, M., Kalkman, V.J., Schneider, W., Samraoui, B., and Cuttelod, A. (2009), *The Status and Distribution of Dragonflies of the Mediterranean Basin*, Gland and Malaga: IUCN.

Selys Longchamps, E. de (1849), 'Troisième famille. Les libelluliens', in *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842*, ed. H. Lucas, Paris: Impremerie nationale, pp. 115−135.

Sugimura, M. (1983), 'Seasonal Body-Size Difference in Some Dragonflies in Southern Shikoku District ES', *Tombo*, 26, 31−34.

Suhling, F. (1995), 'Temporal Patterns of Emergence of the Riverine Dragonfly Onychogomphus Uncatus (Odonata: Gomphidae)', *Hydrobiologia*, 302, 113−118.

Testard, P. (1975), 'Note sur l'émergence, le sex-ratio et l'activité des adultes de Mesogomphus genei Selys, dans le Sud de l'Espagne (Anisoptera: Gomphidae)', *Odonatologica*, 4, 11−26.

Thompson, J.N., and Pellmyr, O. (1991), 'Evolution of Oviposition Behavior and Host Preference in Lepidoptera', *Annual Review of Entomology*, 36, 65−89.

Ubukata, H. (1981), 'Survivorship Curve and Annual Fluctuation in the Size of Emerging Population of Cordulia Aenea Amurensis Selys (Odonata: Corduliidae)', *Japanese Journal of Ecology*, 31, 335−346.

Wesenberg−Lund, C. (1913), 'Odonaten−Studien', *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 6, 373−422.